Initial Impacts and Field Validation of Host Range for *Boreioglycaspis melaleucae* Moore (Hemiptera: Psyllidae), a Biological Control Agent of the Invasive Tree *Melaleuca quinquenervia* (Cav.) Blake (Myrtales: Myrtaceae: Leptospermoideae)

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ABSTRACT   Invasion of south Florida wetlands by the Australian paperbark tree, *Melaleuca quinquenervia* (Cav.) S.T. Blake (melaleuca), has caused adverse economic and environmental impacts. The tree's biological attributes and favorable ambient biophysical conditions combine to complicate efforts to restore and maintain south Florida ecosystems. Management requires an integrated strategy that deploys multiple biological control agents to forestall reinvasion and to supplement other control methods, thereby lessening recruitment and regeneration after removal of existing trees. This biological control program began during 1997 when an Australian weevil, *Oxyops vitiosa* (Pascoe), was released. A second Australian insect, the melaleuca psyllid (*Boreioglycaspis melaleucae* Moore), first introduced during 2002, has also widely established. After inoculation of the psyllid in a field study, only 40% of seedlings survived herbivory treatments compared with 95% survival in controls. The resultant defoliation also reduced growth of the surviving seedlings. A weevil-induced decline at a site comprised mainly of coppicing stumps had slowed after a 70% reduction. Psyllids colonized the site, and 37% of the remaining coppices succumbed within 10 mo. The realized ecological host range of *B. melaleucae* was restricted to *M. quinquenervia*; 18 other nontarget plant species predicted to be suboptimal or nonhosts during laboratory host range testing were unaffected when interspersed with psyllid-infested melaleuca trees in a common garden study. Evaluations are ongoing, but *B. melaleucae* is clearly reducing seedling recruitment and stump regrowth without adversely impacting other plant species. Manifestation of impacts on mature trees will require more time, but initial indications suggest that the psyllid will be an effective supplement to the weevil.

KEY WORDS   weed biological control, plant damage, Florida Everglades, classical biological control, nontarget effects

Melaleuca quinquenervia (Cav.) S. T. Blake (Myrtales: Myrtaceae), the five-veined paperbark tree (hereafter "melaleuca"), is a large (25–30 m tall), native Australian tree of wetland habitats. It naturally occurs within 40 km of the eastern coast of Queensland and New South Wales (11–34° S), with sporadic occurrences in New Guinea and New Caledonia (Boland et al. 1987). Melaleuca was introduced into Florida landscapes during the late 19th century for ornamental purposes (Dray 2003). Its habitat is threatened by coastal development in Australia (Turner et al. 1998), but melaleuca has flourished within its adventive range to become an abundant wetland invader. This is especially true in the fire-maintained ecosystems that typify south Florida (Laroche and Ferriter 1992).

Restoration of melaleuca-invaded habitats is impeded by the plant's inherent capacity to regenerate. In Florida, synchronized flowering events occur during winter (dry season) and to a lesser degree in the summer, although a small proportion may reproduce at unpredictable intervals (Meskimen 1962). Inflorescences are indeterminate, 2–5 cm long, and arranged in bottlebrush-like spikes (Holliday 1989). Persistent capsular fruits arise from flowers and are arranged in a series of clusters, which may remain attached to the trunks, branches, or twigs for several years (Meskimen 1962). Capsules each contain 200–350 minute seeds (Meskimen 1962), and canopy-held seed banks store as many as 51 million seeds per tree (Hofstetter 1991, Rayachhetry et al. 1998). Although a high percentage of the apparent seeds are actually unfilled seed coats, 10–15% consists of embryonic, viable seeds (Rayachhetry et al. 1998). These are released en masse

when fire, felling, or herbicide applications sever vascular connections or otherwise cause desiccation of the capsules. The resultant seed rain produces seedling densities of up to 20 million individuals/ha (Franks et al. 2006). Densities of mixed age-class stands of >36,000 trees/ha have been reported, although this thins to 10,000–15,000 trees/ha in mature stands (Van et al. 2000, 2002). Restoration of invaded wetlands typically involves felling trees in hopes of fostering the return of native species. Melaleuca stumps, however, coppice readily and produce root suckers (Center et al. 2000) that result in stand densities equal to or greater than previous levels, so that felling without follow-up stump treatment is futile (Scoles et al. 2006).

Sustainable melaleuca management depends on removing existing stands while hampering regeneration and preempting reinvasion (Silvers et al. 2007). The role of the biological control program has therefore been to suppress regeneration from felled trees and minimize recruitment in cleared areas by reducing reproduction while increasing seedling mortality. The leaf-feeding melaleuca weevil, *Oxyops vitiosa* (Pascoe) (Coleoptera: Curculionidae), released during 1997 (Center et al. 2000), has served these needs at many locations (Pratt et al. 2005), but expansion of the larval population depends on an abundance of young foliage, which becomes available mainly during late fall to spring. Furthermore, pupation occurs in dry soil, and pupae do not survive prolonged inundation, so they do not thrive in habitats characterized by lengthy hydroperiods. The sap-feeding melaleuca psyllid, *Boreioglycaspis melaleucae* Moore (Hemiptera: Psyllidae), completes its life cycle entirely on the plant (Purcell et al. 1997, Wineriter et al. 2003), so it is not vulnerable to hydrological conditions. It was released during 2002 and has established populations even where *O. vitiosa* cannot. Like all psyllids, *B. melaleucae* passes through five instars (Hodkinson 1974), and development from egg to adult spans 28–40 d (Purcell et al. 1997). Early instars are active, but later stages are more sessile and aggregate on leaves or stems, secreting copious amounts of white, waxy filaments from dorsal glands (Pratt et al. 2004). Adults and nymphs feed by inserting their stylets through stomatal pores to gain access to the phloem (Woodburn and Lewis 1973, Purcell et al. 1997). Although impacts by the melaleuca psyllid are expected to take time to become apparent on mature trees, we questioned how this insect will complement the biological control goals of limiting melaleuca regeneration and recruitment. Therefore, we tested the hypothesis that herbivory by *B. melaleucae* will decrease growth and increase mortality of melaleuca seedlings and cut stumps.

Success of the melaleuca biological control program is not only dependent on population suppression of the weed but also the environmental safety of introduced natural enemies. An underlying assumption of biological control asserts that laboratory-based host-specificity testing accurately predicts the ecological host range of herbivorous arthropods after they have been released in nature. This assumption, however, remains largely unconfirmed for most biological control systems in that a thorough assessment of physiological compared with ecological host range is lacking for most introduced natural enemies (Louda et al. 2005). The majority of the few studies that address this issue monitor for impacts of biological control agents on limited numbers of possible nontarget species years or decades after introduction (Blossey et al. 2001, Schooler et al. 2003). Alyokhin et al. (2001), for instance, observed no nontarget use when surveying for the fly *Acinia picturata* (Snow) in flower heads of seven nontarget species in the Asteraceae that had overlapping distributions with the target weed *Pluchea odorata* L. Cass. (Asterales: Asteraceae). Although these types of assessments integrate realistic plant distributions and densities, they often lack a suitable range of possible host species to adequately compare predicted versus realized host ranges. In contrast, a posteriori hypothesis testing using retrospective analyses based on literature reviews and expert opinions provides insights into general patterns of ecological host specificity and evolution but are inherently biased to a limited number of published studies and nonreplicated observations (Fowler et al. 2000, Pemberton 2000). Alternatively, experimental designs that incorporate replicated and interspersed plantings of test species predicted to be suboptimal or nonhosts during host range testing may provide greater insight to the scalability of physiological to ecological host ranges. We adopted this latter approach using a common garden experiment to test the hypothesis that quarantine-based host range determinations accurately predict *B. melaleucae*'s ecological host range.

Materials and Methods

Impact on Seedling Performance. An experiment was designed to quantify the influence of herbivory by *B. melaleucae* on growth and survivorship of *M. quinquenervia* seedlings. Fifteen 0.25-m^2 plots were delineated within a thicket of seedlings during November 2002. All but six randomly selected seedlings were manually removed from each plot. Screened cages were positioned over 10 plots; the 5 noncaged plots were used to monitor the effect of cages on seedling growth. The cage frames were ≈0.75 m in height and covered with a lightweight, tightly woven "no-see-um" nylon mesh screen (246 holes/cm^2). The bottom edge of each cage was buried in the soil, whereas the cage top was closed with a knot. Observations within a cage took place by untying the knot to slide the screen down along the frame.

Five replicate plots, each containing six seedlings, were randomly assigned to one of three treatments: herbivore release, caged control, or uncaged control. The herbivore treatment involved transference of 15 first and second instars to each plant within each cage on 6 December 2002. This approximated threshold densities needed to induce an effect on seedlings of similar size as determined by Franks et al. (2006). To maintain consistent herbivore population densities, several sticky traps placed in each cage entangled the

adult psyllids as they emerged. Adults not caught by the sticky traps were manually removed as needed. Additional inoculations of nymphs were made on 19 February and 16 April 2003 after the original psyllids had completed development. The height of each seedling was measured, and numbers of leaves per seedling were counted in each plot at monthly intervals. Height was measured from the soil level to the apical tip of the most distant living shoot. Above- and below-ground biomass was also assessed before the onset of the experiment by randomly uprooting one of the six seedlings in each plot and quantifying stem, foliar, and root biomass, as well as stem diameter at the soil level. This procedure was repeated a second time in February and again at the end of the study for the four remaining seedlings. The influence of herbivory on seedling growth rate, leaf number, and plant-partitioned biomass was compared over time with repeated measures analysis of variance (ANOVA) (von Ende 1996). The Huynn-Feldt adjustment was used when the covariance matrix did not meet the assumption of sphericity (SAS Institute 1999, Littell et al. 2002a). Differences in seedling status and survivorship among treatments were compared with ANOVA. To meet assumptions of normality and homogeneity of variances implicit in the parametric analysis, the arcsine transformation $(\sin - 1[[\mathrm{rad}]\mathrm{y}])$ was applied to frequency data before analysis.

Impact on Coppicing Stumps. Censuses had been ongoing at a study site near Estero, FL, since October 1998 at ≈6-wk intervals to estimate *O. vitiosa* population densities (Center et al. 2000). Psyllids, which were released on 18 March 2002, were included in the counts beginning on 5 December 2002 (262 d postrelease), but data on the frequency of occurrence (presence/absence) were collected beginning from the previous May. Subsequent sampling (done on 22 January, 7 March, and 23 April 2003) terminated when the site was disrupted for commercial development. The point-quarter distance method, normally used in forestry to estimate tree density, also seemed appropriate for stumps, so the number of live coppices was estimated using this technique (Krebs 1999). Sampling involved selecting a series of points, in this case by randomly selecting grid intersection points, and then partitioning the area surrounding each point into quadrants (NE, SE, SW, and NW). Distance from the point to the center of the nearest live coppice in each quadrant was measured to the nearest centimeter. A 20 by 20-m grid (Center et al. 2000) was used to randomly select 50 sampling points. Tree density was determined from the formula:

$$\hat{N}_p = 4(4n - 1)/\pi\Sigma(r^2_{ij}) \qquad \text{(Krebs 1999)}$$

Where $\hat{N}_p$ = the estimate of population density, n = the number of random points, and r_{ij} = the distance (in meters) from point i to the nearest coppice in quadrant j. This provided an estimate of the coppice density (plants/m^2), which was multiplied by the site area to determine the total number of coppices within the delimited sector (8.09 ha). Plant injury caused by psyllids was rated on a six-point scale according to the proportion of the foliage affected (0 = no damage; 1 = <25%; 2 = 25–49%; 3 = 50–74%; 4 = ≥75%; 5 = no green foliage remaining). The presence or absence of psyllid eggs was noted on each coppice, and the number of psyllid adults and branch tips were tallied.

All above-ground biomass was harvested from 25 randomly selected coppices at each sampling interval. These samples were transported to laboratory facilities where 10% of the stems were subsampled to count nymphs. Leaves were individually removed and microscopically examined. Numbers of nymphs were tallied according to their stage of development (early and late instars). The density per plant was estimated by multiplying the number of nymphs per stem by the number of stems per plant. The total nymph and adult populations on site were determined by multiplying this product by estimates of the number of live coppices at the site. The leaves were removed from all of the plants and sorted according to whether they were young or old and dried at 70°C. Leaf mass was determined gravimetrically to the nearest gram, and the quantity present on site was similarly extrapolated to assess resource availability.

Nontarget Impacts. An experiment was designed to quantify the ecological host range and unintended impacts of *B. melaleucae* on plant species that ranged from suboptimal to nonhosts for the psyllids during earlier quarantine testing (Wineriter et al. 2003). The study, conducted at the USDA–ARS Invasive Plant Research Laboratory in Davie, FL, involved a common garden plot in which rows of "at risk" species were planted to alternate with rows of *M. quinquenervia* trees. Four *M. quinquenervia* saplings (≈1 m tall) were planted in 11 rows each, with individuals separated by 7.6 m within and between rows. Four replicates of 18 test species were planted in a randomized block design among the *M. quinquenervia* rows (Table 1). A row of nine randomly selected test plants was established between each *M. quinquenervia* row, with two test plant rows comprising a block. Beginning in August 2002, each test plant and *M. quinquenervia* tree was carefully inspected at monthly intervals (except September and April) when the number of adult psyllids and discrete nymphal colonies were recorded. The influence of plant origin (exotic versus native) and phylogenetic relatedness to the target species (*Melaleuca* and *Callistemon* spp. versus others) on incidence of adult *B. melaleucae* recruitment to the test plants were compared with logistic ANOVA (PROC GENMOD; Littell et al. 2002b).

Results

Impacts on Seedling Performance. Cages had no discernible effect on measured parameters (number of leaves: $F_{1,8} = 1.17; P = 0.3547$, height: $F_{1,8} = 0.96, P = 0.3547$), so control data were pooled and compared with the herbivory treatment. Herbivory by *B. melaleucae* increased defoliation of seedlings when assessed over the entire study period ($F_{1,13} = 7.72; P < 0.0157$). Defoliation levels fluctuated temporally (time × leaf number: $F_{5,65} = 6.64; P = 0.0032$), how-

Table 1. Host range verification of *B. melaleucae*

Species	Family	Origin[a]	Predictions[b]	Realized densities	
				Adult[c]	Nymph[c]
Callistemon citrinus	Myrtaceae	Exotic	+	0.00	0
Calyptranthes pallens	Myrtaceae	Native, FT	−	0.24	0
Calyptranthes zuzygium	Myrtaceae	Native, FE	−	0.00	0
Eugenia axillaris	Myrtaceae	Native	−	0.00	0
Eugenia confusa	Myrtaceae	Native, FE	−	0.04	0
Eugenia foetida	Myrtaceae	Native	−	0.06	0
Eugenia rhombea	Myrtaceae	Native, FE	−	0.00	0
M. quinquenervia	Myrtaceae	Exotic	+++	Abundant	84.63
Melaleuca rigidis	Myrtaceae	Exotic	++	0.04	0
Melaleuca viminalis	Myrtaceae	Exotic	+	0.14	0
Myrcianthes simpsonii	Myrtaceae	Native, FT	−	0.00	0
Myrciaria cauliflora	Myrtaceae	Exotic	−	0.02	0
Myrica cerifera	Myricaceae	Native	−	0.00	0
Pimenta dioica	Myrtaceae	Exotic	−	0.04	0
Pimenta racemosa	Myrtaceae	Exotic	−	0.00	0
Psidium guajava	Myrtaceae	Exotic	−	0.00	0
Psidium longipes	Myrtaceae	Native, FT	−	0.04	0
Syzygium jambos	Myrtaceae	Exotic	−	0.04	0
Syzygium malaccense	Myrtaceae	Exotic	−	0.04	0

[a] Exotic or native to Florida, U.S. species considered threatened or endangered in Florida are designated as FT and FE, respectively.

[b] Quarantine-based host specificity tests predict that nymphs of *B. melaleucae* would fail to establish (−), survive 7 wk on test plant (+), compete development (++), and persist for multiple generations (+++) (Wineriter et al. 2003).

[c] Represents the total no. adults or discrete nymphal colonies encountered per plant over entire study period (5 replicates × 10 sampling events = 50 assessments). Adults were not quantified for *M. quinquenervia* because of sampling inaccuracies attributed to rapid within plant dispersal.

ever, as herbivory-induced leaf drop stimulated expansion of dormant basal buds, which initially increased leaf numbers (Fig. 1c). Although numerically similar after 5 mo, leaves derived from adventitious buds were smaller than their counterparts and were quickly exploited by the herbivores soon after bud elongation, resulting in a second defoliation event (Fig. 1c). Plant height remained constant among treatments over the first four sample dates, after which reduced seedling height was observed ($F_{1,13} = 199.0; P < 0.0001$; Fig. 1b). Herbivory also resulted in progressively greater levels of stem death over time ($F_{5,65} = 91.70; P < 0.0001$). Consistent with measured parameters, herbivory led to experiment-wise reductions in leaf (Fig. 1a; $F_{1,9} = 6.32; P < 0.0001$), stem ($F_{1,9} = 6.32; P < 0.0001$), and root ($F_{1,9} = 5.35; P < 0.0459$) biomass. Mortality was 12-fold greater among herbivore-damaged seedlings ($F_{1,14} = 15.25; P < 0.0018$), with 60% succumbing in herbivory treatment plots in contrast to only 5% mortality in untreated control plots.

Impact on Coppicing Stumps. The periodic mowing at the Estero site induced root suckering that tended to increase coppice density. We estimated on 15 October 1998 that 51,360 live coppices existed at the site. As the *O. vitiosa* (released 8 October 1997) population increased, however, the number of sprouting coppices steadily decreased. The quantity on site had diminished to ~15,000 by November 2001 and to 12,800 by December 2001. Although estimates fluctuated, they remained within this range for over a year (Fig. 2). We first observed psyllids within the pasture, but on <1% of the coppices, during May 2002, ≈2 mo after their release. The coppice density had increased to 16,734 by October, the highest count since August 2001. However, psyllid populations had also steadily in-

creased and dispersed until they infested 100% of the coppices by year's end. The number of live coppices then declined to 12,703 as the psyllid population rose to over 193,000 adults and 2.2 million nymphs. Psyllid numbers peaked in January 2003 at 715,581 adults and 10.9 million nymphs; the estimated number of coppices declined further to 10,754. Damage to the remaining coppices was heavy with 43% rated at level 3 (50% of the foliage affected) or above. This increased further during the spring, and by March, 85% of the foliage was rated as damaged at or above level 3. The estimate of 9,429 live coppices during April 2003, when monitoring was forced to terminate, represented the lowest density ever recorded at the site. This represented 18% of the coppices present during October 1998 and 56% of those present during the previous October. The psyllid population had correspondingly declined to an estimated 324,943 adults and 4.7 million nymphs, mainly because of the reduced carrying capacity. We estimated that only ≈15.1 kg (dry weight) of suitable foliage was available at the site as of April 2003 compared with ≈99.7 kg during March 2001.

Nontarget Impacts. *Boreioglycaspis melaleucae* readily colonized *M. quinquenervia* trees in the study plot, 92% of which harbored psyllids during the first sampling episode. The number of discrete nymphal colonies averaged 86 ± 16.97 colonies per tree and ranged from an initial 68 ± 31.44 colonies at the beginning of the study to 146 ± 54.98 per plant at the conclusion (Fig. 3). Adult psyllids did alight on leaves of nontarget plants, but no eggs or nymphal colonies occurred on the test species (Table 1). The occurrence of adult psyllids was not influenced by the plant's origin ($\chi^2_1 = 1.28, P < 0.258$) or phylogenetic relatedness to *M. quinquenervia* ($\chi^2_1 = 0.64, P = 0.4246$), suggesting that
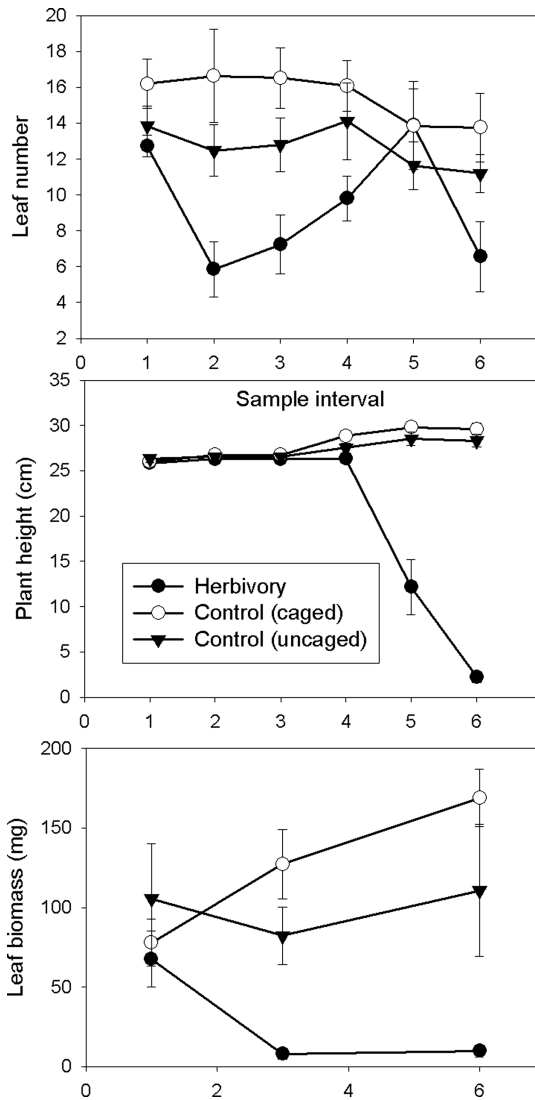
Fig. 1. Herbivory by *B. melaleucae* reduced (a) the number of leaves per *M. quinquenervia* seedling, (b) seedling height as measured from the soil line to the apical meristem, and (c) the total leaf biomass. Herbivory and control treatments were conducted under caged conditions, whereas the cage control represents data from uncaged seedlings.

adult incidence was randomly distributed across all nontarget plants within the study area. This showed ample opportunity for psyllids to colonize nontarget species, but they failed to do so. No feeding damage, honeydew, or other signs of colonization were observed on any nontarget species, not even on congeners, despite careful monthly inspections.

Discussion

Drainage of Florida's Everglades during the last century provided newly created habitat for many invasive plants. Foremost among these was the Austra-
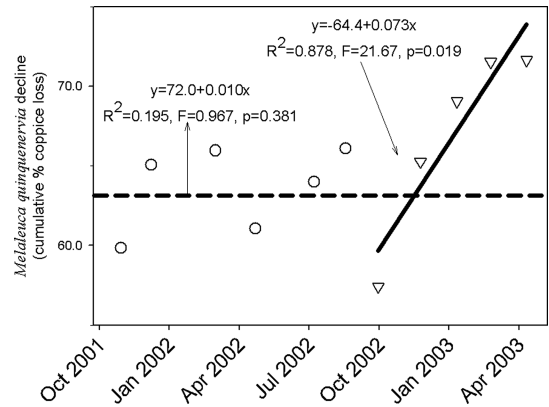

Fig. 2. The cumulative decline of coppicing stumps at the Estero site. The impact of *O. vitiosa* had stabilized as shown by the dashed base line, but coppice mortality had begun to increase again after the psyllids colonized the site.

lian paperbark tree *M. quinquenervia*. Its rampant invasion of native plant communities now complicates restoration of Everglades wetlands, which had focused on restoring natural water flow patterns and periodicity (Ogden 2005). As a result, management agencies now must consider vegetation management while reestablishing hydrological regimens if restoration is to succeed. Biological control, as integrated within an overall melaleuca management program, was envisioned as a means to lessen regeneration after removal of existing trees and as a mechanism to forestall reinvasion. Accordingly, the biological control program, which started during 1997 on the release of the weevil (*O. vitiosa*), continued with the release of the melaleuca psyllid (*B. melaleucae*).

One of the most obvious impacts of the psyllids involved the premature abscission of mature leaves. Infested leaves after being colonized by psyllids pro-
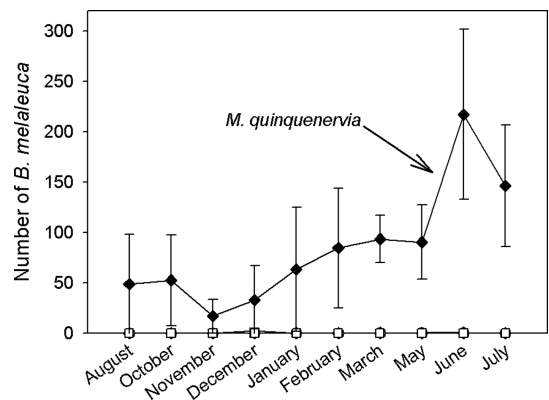

Fig. 3. The numbers of discrete psyllid nymphal colonies on *M. quinquenervia* trees compared with the numbers of psyllid adults on "at-risk" plant species in a common garden plot study. Adults were too numerous and flighty to count on melaleuca but a few occasionally alighted and were counted on the nonhosts. Nymphs were never found on anything but *M. quinquenervia*.

gressively change color from green to red to brown before detaching from the branch (Morath et al. 2006). This process occurs relatively rapidly and is thought to be caused by phytotoxic salivary exudates injected by the psyllids (Hodkinson 1974) and resembles the degeneration associated with senescing leaves (Crawford and Wilkens 1996). As a result, infested trees appeared progressively denuded. This accentuates the effects of the weevils that defoliate young foliage from stem tips. The combined stress caused by these two insect species has markedly reduced melaleuca flowering and seed production throughout southern Florida (Pratt et al. 2005), which was a primary objective of the melaleuca biological control program.

In addition to lessening reproduction, biological control was expected to limit reinvasion by suppressing seedlings. As with many species, seedlings likely represent a sensitive transitional stage in the life cycle of *M. quinquenervia.* For invasive woody species, seedlings have substantially less leaf area and reserve carbon storage and may be far more vulnerable to attack by biological control agents than mature trees (Franks et al. 2006). Herbivory by *B. melaleucae* reduced seedling survival by 55% within three generations, showing that psyllids can kill new germinants and further decreasing the likelihood that melaleuca will regenerate after being cleared from a site. It remains unclear, however, if these effects will translate into reductions in population growth rates and spread of melaleuca invasions. The lack of a long-lived soil seedbank (Van et al. 2005), for instance, makes *M. quinquenervia* particularly vulnerable to herbivore-mediated reductions in fitness and delays in reproductive maturation. As canopy-held seedbanks continue to diminish over time (Pratt et al. 2005), seedling suppression is predicted to have direct, long-term effects on plant density. To test this prediction, future research will examine how herbivores affect stage-specific demographic transitions of melaleuca and quantify the effects of herbivory within the context of the entire plant life cycle (Doak 1992, Shea and Kelly 1998).

Because of the impact of the two insect species, melaleuca now suffers repeated defoliation-refoliation cycles similar to that described by Ohmart and Edwards (1991) for eucalypts in Australia. In eucalyptus species, defoliation events are followed by refoliation from leafy shoots produced from axillary buds, accessory buds, epicormic buds, and possibly lignotubers. Melaleuca, being closely related to eucalypts, is probably similar. Repetition of this cycle can lead to dieback. Increased nutritional quality of regrowth foliage on trees suffering dieback leads to additional episodes of intense herbivory. As a result, the cycle becomes self-perpetuating and depletes the starch reserves of the trees ultimately causing them to succumb. This defoliation-refoliation model probably explains the coppice decline that we observed at Estero.

The decline of coppicing stumps, such as that observed at the Estero site, is also likely to enhance management programs. Approximately 51,000 stumps

were present during October 1998, and the number had been increasing in response to mowing-induced root suckering. Numbers began to decline, however, after release of *O. vitiosa*, presumably because of the combination of herbivory and mowing. The weevils did not kill the stump regrowth outright, but fewer stumps resprouted after each mowing. Only 15,000 coppicing stumps remained as of November 2001, by which time the number had stabilized (Fig. 2). The lack of further impact was likely related to the size of the stumps. Larger stumps with more extensive root systems are likely to have greater carbohydrate reserves. As a consequence, they may be better able to regenerate than the smaller ones (Kruger and Reich 1993 a, b). This stalled decline resumed after psyllids fully colonized the site. In contrast to the effect of the weevils, many psyllid-laden coppices appeared dead having a burnt visage, with desiccated, brown foliage and dry, brittle stems. The density of living coppices decreased to ≈9,400 by April 2003, 40% of which seemed on the verge of dying, although not yet dead. We were not able to track further declines having been forced to terminate the study when the property was sold to a developer. However, this suggested that the combination of mechanical removal and biological control could provide an effective integrated control approach with lessened need for herbicidal treatment of cut stumps to prevent regrowth. More rigorous empirical studies have now been initiated and are validating these observations.

An essential component to preintroduction evaluations of potential biological control agents involves quantifying the host range of natural enemies as a method for assessing the inherent risk they pose to native and economically important flora. In the absence of corroborative postrelease data, criticisms have been raised concerning the accuracy of laboratory-based host range predictions and nontarget ecological interactions in weed biological control programs (Louda et al. 2005, Pearson and Callaway 2005). To test the host range predictions for *B. melaleucae*, 18 test plant species, ranging from suboptimal to nonhosts, were interplanted with *M. quinquenervia* in an experimental garden (Table 1). We determined that nontarget plant species postulated to be at risk, *Melaleuca* and *Callistemon* species (Myrtales: Myrtaceae), experienced levels of adult psyllid recruitment similar to more distantly related species (Table 1). We observed no oviposition, feeding, or colonization of nontarget plants by *B. melaleucae*, even though herbivore population densities were of sufficient magnitude to adequately challenge nontarget species. These results lend additional support to the premise that risk assessments based on physiological host ranges, as characterized by laboratory testing, are conservative compared with the realized ecological host ranges that occur under field conditions (van Klinken 2000, Littlefield and Buckingham 2004, Delfosse 2005).

Psyllids are well known as damaging pests (Hodkinson 1974, Burts 1988, Brennan and Weinbaum 2001, Tsai et al. 2002) and tend to be evolutionarily constrained to phylogenetic host lineages, often to one

host plant species or species within a single genus (van Klinken 2000). Given their ability to damage plants and their narrow host range, it is surprising that psyllids have seldom been used in biological control programs. *B. melaleucae* is only the fourth psyllid species released for biological control of a weed. *Arytainilla spartiophila* (Förster) was released in New Zealand and Australia against Scotch broom, *Cytisus scoparius* L. Link (Fabales: Fabaceae), and *Heteropsylla spinulosa* Muddiman, Hodkinson, and Hollis was released in Australia and on several Pacific islands in an attempt to control creeping sensitive plant [*Mimosa invisa* Martius (Fabales: Fabaceae)] (Julien and Griffiths 1998). *Prosopidopsylla flava* Burkhardt was released against mesquite [*Prosopis* spp. (Fabales: Fabaceae)] in Australia during 1998 (van Klinken et al. 2003). Although the impacts of these species are generally unknown, *A. spartiophila* has produced excellent control of *M. invisa* in Papua New Guinea (Kuniata and Korowi 2004).

The impact of *B. melaleucae* on coppices and seedlings is clear, but effects to large trees remain to be shown. Evaluations are ongoing, but early indications suggest that *B. melaleucae* will be a safe and effective agent that will complement the effects of the earlier introduced weevil.

Acknowledgments

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